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SOME HOST-PARASITE RELATIONS IN THE BLACK ROOT ROT OF APPLE TREES [1]

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INTRODUCTION

In investigating black root rot, the writer began with studies of the causal fungus (*Xylaria mali* Fromme), but as the work progressed to a study of conditions affecting infection the host-parasite relations when the hosts were growing under normal and abnormal conditions assumed greater importance. In this paper are reported the results of inoculating apple seedlings (*Malus pumila* Mill.) with *X. mali* at monthly intervals; the effects of defoliation and other maltreatments on susceptibility of apple are also reported.

METHODS

Unless otherwise stated, the method of inoculation consisted in uncovering root tissue below the collar of the tree, wounding by cutting or scraping the bark, placing a piece of inoculum in the wound, and finally replacing the soil. At first, inoculations were made through flaps cut entirely through the bark, but later experiments showed that deep wounding was not necessary or desirable. Beginning in 1934, the wounds were made by merely scraping the bark of the root with a trowel. The inoculum consisted of heat-sterilized apple twigs about 2 inches long, on which the pathogen had been grown for at least 2 months. Some of the trees used were grown for an experimental period of 2 to 6 years in nurseries at the Arlington Experiment Farm, Arlington, Va., or at the Plant Industry Station, Beltsville, Md. Since infection did not occur on uninoculated trees or even on the uninoculated part of inoculated roots, it was considered unnecessary to leave part of each plot uninoculated as a check on infection.

Each year, after killing frosts had occurred in the autumn, the soil at the point of inoculation was removed, the number of infections counted, and the length and the breadth of the lesions measured. As in an earlier report on black root rot (*1*),[2] the sizes of lesions were computed in the following manner. For each lesion the length was multiplied by the breadth to determine the approximate area. The square root of the resultant value was then derived, giving a linear value equal to one side of a square having an area approximating that of the lesion. The values recorded in the tables are averages of such relative linear functions for all lesions in each designated plot.

[1] Received for publication May 5, 1943.

[2] Italic numbers in parentheses refer to Literature Cited, p. 457.

EFFECT OF INOCULATING SEEDLINGS AT MONTHLY INTERVALS

In the earlier inoculation experiments irregular and often negative results had been obtained. It was thought that such results might be due to inoculating at the wrong time of the year. For this reason a series of inoculations made at monthly intervals was started in the spring of 1932 and continued until November 1935. At the beginning of the experiment the trees were seedlings growing their second season in nursery rows at the Arlington Experiment Farm. Twenty to thirty trees were inoculated at as nearly the middle of each month as was practicable.

In 1932 inoculations were made with culture 3, but all subsequent inoculations were made with culture 57. The trees were too small in 1932 for crowding to be serious or moisture to be deficient, but this was not the case in later years. No infections resulted from the use of culture 3. The results with culture 57 for 3 consecutive years are recorded graphically in figure 1.

The results of the 1932 inoculations, all of which were negative, appeared at first to be aberrant, but there were certain conditions which at least partly account for these results. The trees were young, vigorous, and not crowding one another, and the season was favorable for growth. It is significant that, when the trees inoculated in 1932 were examined in August of that year, there were small lesions 3 to 5 mm. in diameter on some of the trees inoculated in July but none on those inoculated in any other month. By October or November the small lesions observed in August had healed over, leaving only scars; they were then recorded as not infected. The effect of host condition on infection is further shown by another experiment in which some bearing trees in an abandoned orchard at Arlington Experiment Farm were inoculated in August 1932 in a parallel series and with the same isolate (No. 3) used for the inoculations of yearling nursery trees. The inoculations of these old trees resulted in a fair percentage of infections, and lesions as long as 110 mm. were produced.

In 1934 and 1935, which were the fourth and fifth growing seasons for the young trees, conditions were apparently much more favorable for infection than in previous years. In general, a much higher percentage of infection resulted from the June and July inoculations than from those made at any other time. The percentages of infection for 1933 to 1935 rose in June, reached their peak in July, and declined to less than 10 percent by September. Susceptibility at any particular date may differ from season to season. For example, infection for August 1934 was 57 percent, but for August 1935 it was only 9 percent. The July infections were 83 and 88 percent, respectively, in the 2 years. These records indicate that conditions were favorable for the extension of the infection period into August in 1934 but not in 1935.

Since *Xylaria* has a fairly high optimum temperature, about 25° C. (77° F.), when growing in artificial culture, it is possible that the increase in infection in June and the decline in August may have been due to soil temperatures favorable for the fungus in June and July and unfavorable during the rest of the summer. However, infection of dug apple seedlings has been obtained by the writer (*1*) at a temperature as low as 15° C.

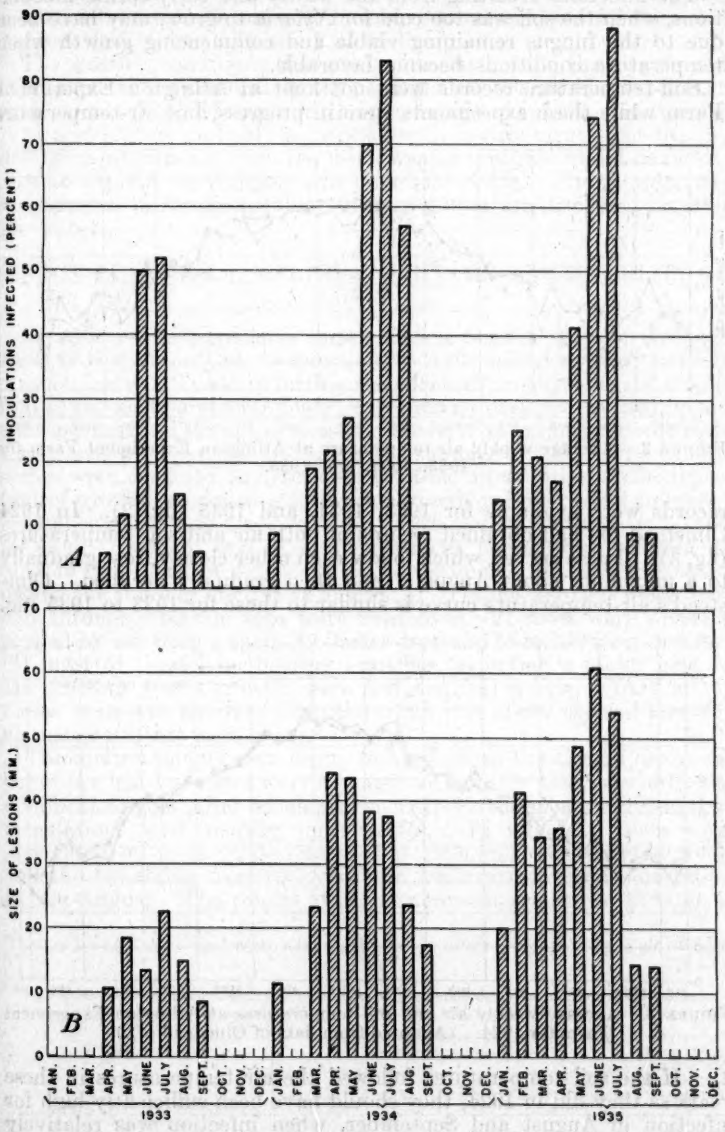

FIGURE 1.—Infection results from monthly inoculations of young apple trees with *Xylaria mali*. *A*, Average percentage of inoculations resulting in infections on the same trees in the months indicated in 3 consecutive years. *B*, Average size of lesions represented in *A*. The size is expressed as a side of a square having approximately the area of the lesion.

The infections resulting from the winter and early-spring inoculations, when the soil was too cold for *Xylaria* to grow, may have been due to the fungus remaining viable and commencing growth when temperature conditions became favorable.

Soil-temperature records were not kept at Arlington Experiment Farm while these experiments were in progress, but air-temperature

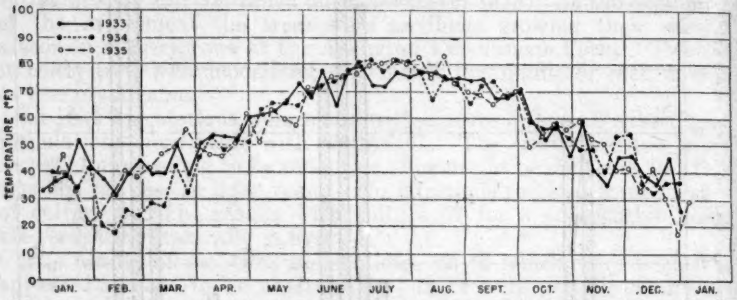

FIGURE 2.—Average weekly air temperature at Arlington Experiment Farm for 1933, 1934, and 1935.

records were available for 1933, 1934, and 1935 (fig. 2). In 1924 Olmstead (*5*) had obtained records of both air and soil temperatures (fig. 3). These curves, which follow each other closely, rose gradually to a maximum about August 1 and then gradually declined. Olmstead's air-temperature curve is similar to those for 1933 to 1935 (fig.

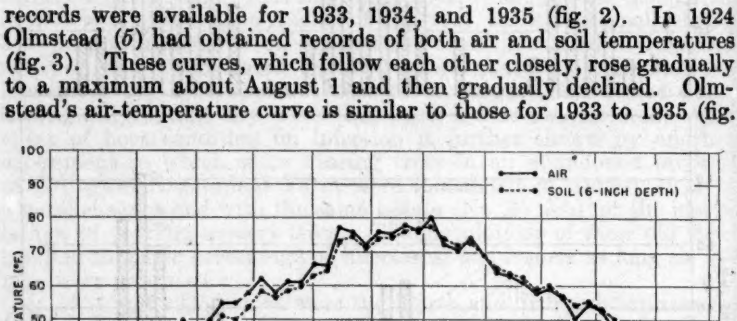

FIGURE 3.—Average weekly air and soil temperatures at Arlington Experiment Farm for 1924. (Adapted from data of Olmstead (*5*).)

2). If the soil temperatures followed the air temperatures in these years as they did in 1924, they should have been sufficiently high for infection in August and September, when infection was relatively slight. This suggests that some factor other than temperature change may have been responsible for the little infection found.

The weather record for Arlington Experiment Farm for 1934 shows in average air temperature for July and August of 77° F. and 73.8°,

respectively, and for 1935, 80.2° and 77.9°. The rainfall for July and August 1934 was 1.79 and 5.07 inches, respectively, and for July and August 1935 it was 2.77 and 2.25 inches.

The weather conditions that predispose the host to the disease and that favor the development of the pathogen are too complex for proper evaluation. The difference in the percentage of infection in August 1934 and 1935 is probably associated with environmental conditions, but more information than the usual weather records would be necessary to explain the difference in infection trends. The factors contributing to high susceptibility in midsummer are discussed later in the paper.

EFFECT OF SEASONAL MALTREATMENTS ON SUSCEPTIBILITY OF HOST

Periodic inoculations have shown that at certain times of the year apple is very susceptible to infection by *Xylaria* and at other times it is much less so. To study further the effect of the physiological condition of the host on susceptibility, experiments designed to modify the translocation and storage processes of the host by various periodic maltreatments were carried out during the summer of 1936. The experiments were designed to determine whether interruption or modification of growth processes at different growth periods would influence resistance of roots to black root rot. Five plots of 20 to 30 trees each for each treatment and at each treatment period were selected at random in a block of 4-year-old apple seedlings. Plots were treated during the summer months as follows: (1) Trunks were cut more than half through, and the tops were bent over; (2) roots were severely pruned by inserting a spade 12 inches deep and 15 inches from the tree; (3) most of the foliage-bearing branches, including a major part of the previous year's growth, were removed; (4) a ring of bark about 6 mm. wide was removed from the trunk just above the soil line; (5) no maltreatments were given.

The maltreatments were begun in April about the time of the swelling of the leaf buds and were repeated at monthly intervals until the middle of August, after which previous experiments had indicated that inoculations were usually unsuccessful. In mid-July roots were inoculated on trees treated up to that time and on untreated trees, and the remaining trees received both maltreatment and inoculation in mid-August. The results of this experiment are shown in table 1.

TABLE 1.—*Effect of maltreatments in different months on infection by Xylaria mali in 1936*

[20 to 30 trees inoculated in each treatment on each inoculation date; results taken in November]

Treatment	Trees infected when inoculated on July 14 but treated on indicated date					Trees infected when treated and inoculated on August 14
	April 8	May 8	June 5	July 8	July 14	
	Percent	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*
None (check)	76	76	76	76	76	55
Trunk cut and bent	91	90	96	85	93	81
Roots pruned	85	50	86	----	----	----
Trunk ringed	100	100	94	89	87	----
Branches summer-pruned	----	75	91	84	84	90

Table 1 shows in general slightly less infection on the unwounded trees than on those receiving the maltreatments. These differences were usually more pronounced when maltreatments were given in June and inoculations were made in July than when maltreatments were given in July and inoculations made in July. The differences, however, between the untreated trees and maltreated trees were not as great as might have been expected from such harsh treatment. For the trees receiving no maltreatments the average size of lesion for July inoculation was about 35 mm.; for the maltreated trees the average sizes for the different periods of treatments ran from 40 to 45 mm.

Since root pruning was difficult to carry out in dry gravelly soil it was discontinued after June. Root pruning in the main showed the same tendency to increase infection as the other maltreatments. However, the number of infections was low on the trees root-pruned in May.

Ringing gave more irregular results than any other treatment. If the girdle was partially closed by callus and the bark was not directly killed by girdling, very large lesions resulted from inoculations made 3 to 4 inches below the girdle. However, if the girdle was not partially closed by callus, the bark usually died below the girdle and the dying extended to the inoculation or below it. In such cases the black root rot lesions were usually small but distinguishable from the adjacent necrotic tissue by their intense black color. Apparently, as general necrosis approached the inoculation point the advance of the fungus was impeded or stopped. Possibly with death of the host tissue some substance toxic to the fungus developed. However, observations by the writer have shown that when the fungus attacks and kills living roots it may remain alive long after the death of the host. The general trend of the results of maltreatments was a slight increase in the percentage of trees infected and in the size of lesions as compared with trees not maltreated.

EFFECT OF DEFOLIATION ON SUSCEPTIBILITY OF HOST

The experiment just described showed that summer pruning involving considerable loss of leaves increased the susceptibility of the host to *Xylaria*. Defoliation by leaf removal modifies food synthesis and associated processes with less mutilation than defoliation by summer pruning. The drastic effect of defoliation on the periodic interdependence of root and top would be expected to affect the susceptibility of the roots to this disease.

Preliminary experiments with defoliation by leaf removal were begun in the summer of 1934 on 2-year-old apple trees in a nursery at Arlington Experiment Farm. The results indicated a possible relation between defoliation and susceptibility. In these preliminary experiments the trees defoliated in August had a higher percentage of infection and larger lesions than the nondefoliated check trees.

In 1937 an experiment was begun to study the effect on root susceptibility of defoliating trees at different times throughout the growing season. Three-year-old Stayman Winesap trees worked on seedling roots were set 2 feet apart in rows 4 feet wide and divided into plots of 20. Randomized plots were defoliated at semimonthly intervals from May 3 to October 18, that is, from the time when young shoots were 3 to 4 inches long until the leaves had been frozen. Since previous experience had shown July to be the most favorable period for infection by *Xylaria*, the first inoculation of 1937 was made on July 15

on the previously defoliated plots and on one nondefoliated (check) plot. For the remainder of the season inoculations were made at the time of each semimonthly defoliation; nondefoliated (check) plots were inoculated at the same time. In order to allow a reasonable period for root rot development, recording of infections was delayed until April 1938.

In 1938 the treatments were repeated on all the plots on essentially the same dates as in 1937; inoculations were made on the opposite side of the trees, and the record of infections was taken the following spring. Defoliations were not repeated in 1939; but all trees were inoculated in mid-July, and the results were recorded at the end of the growing season. The results of the experiment are recorded in table 2.

TABLE 2.—*Effect of defoliation on susceptibility of Stayman Winesap apple trees to Xylaria mali*

Date of first defoliation	Date of second defoliation	Date of inoculation	Trees infected			Size of lesion
			Total infection	Cortical infection	Deep infection	
			Percent	*Percent*	*Percent*	*Mm.*
May 3, 1937		July 15, 1937	33	19	14	16
	May 3, 1938	July 15, 1938	95	0	95	28
		July 15, 1939	94	19	75	31
May 18, 1937		July 15, 1937	34	4	30	18
	May 18, 1938	July 15, 1938	94	0	94	27
		July 15, 1939	88	6	82	24
June 3, 1937		July 15, 1937	45	20	25	13
	June 3, 1938	July 15, 1938	85	5	80	20
		July 15, 1939	90	20	70	24
June 18, 1937		July 15, 1937	40	5	35	15
	June 18, 1938	July 15, 1938	90	5	85	28
		July 15, 1939	89	21	68	23
July 3, 1937		July 15, 1937	50	17	33	14
	July 2, 1938	July 15, 1938	78	0	78	21
		July 15, 1939	94	12	82	31
July 15, 1937		July 15, 1937	21	5	16	37
	July 15, 1938	July 15, 1938	75	18	57	22
		July 15, 1939	89	18	71	32
Not defoliated		July 15, 1937	21	5	16	12
		July 15, 1938	79	10	69	29
		July 15, 1939	91	23	68	24
Aug. 3, 1937		Aug. 3, 1937	45	0	45	18
	Aug. 3, 1938	Aug. 3, 1938	88	13	75	21
		July 15, 1939	100	16	84	30
Not defoliated		Aug. 3, 1937	29	6	23	12
		Aug. 3, 1938	59	35	24	13
		July 15, 1939	100	0	100	34
Aug. 18, 1937		Aug. 18, 1937	20	5	15	16
	Aug. 18, 1938	Aug. 18, 1938	64	24	40	15
		July 15, 1939	95	20	75	29
Not defoliated		Aug. 18, 1937	5	0	5	11
		Aug. 18, 1938	44	21	23	13
		July 15, 1939	84	17	67	28
Sept. 3, 1937		Sept. 3, 1937	33	19	14	15
	Sept. 3, 1938	Sept. 3, 1938	33	33	0	0
		July 15, 1939	57	19	38	17
Not defoliated		Sept. 3, 1937	44	10	34	12
		Sept. 3, 1938	37	37	0	0
		July 15, 1939	74	26	48	18
Sept. 18, 1937		Sept. 18, 1937	34	29	5	17
	Sept. 19, 1938	Sept. 19, 1938	39	39	0	0
		July 15, 1939	71	14	57	22
Not defoliated		Sept. 18, 1937	15	10	5	7
		Sept. 19, 1938	50	15	35	15
		July 15, 1939	89	21	68	26
Oct. 2, 1937		Oct. 2, 1937	6	0	6	8
	Oct. 2, 1938	Oct. 3, 1938	42	38	4	8
		July 15, 1939	92	45	47	19
Not defoliated		Oct. 2, 1937	0	0	0	0
		Oct. 3, 1938	29	25	4	11
		July 15, 1939	96	38	58	24
Oct. 18, 1937		Oct. 18, 1937	21	21	0	0
	Oct. 18, 1938	Oct. 18, 1938	21	21	0	0
Not defoliated		Oct. 18, 1937	0	0	0	0
		Oct. 18, 1938	22	22	0	0

In recording inoculation results it seemed desirable to separate the deep lesions from the shallow ones in which the cortex only was involved. In the cortex type of lesion the fungus began to kill near the surface but did not kill as deep as the cambium; hence, the lesion healed over soon after active growth started. The deep lesions are probably much more important than the shallow ones, and therefore in table 2 the values for deep lesions rather than those for total infection should probably be given the main consideration in evaluating the results.

There was relatively little deep infection in 1937; but other inoculation experiments in that year also gave a low percentage of infection, indicating that that season was unfavorable for infection by *Xylaria*. The trees at that time were only in the third year from planting and were not crowding. Possibly the low infection of 1937 on defoliated and nondefoliated trees was due both to unfavorable conditions for the growth of *Xylaria* and to favorable conditions for growth of the host. A comparison of the percentages of deep lesions on the defoliated and the nondefoliated trees shows a tendency for infection to be more severe on the defoliated than on the nondefoliated trees.

The results were somewhat more striking the second year (1938), when sufficient disease developed to show considerable differences between treatments. Infection was heavy on all trees, but the highest percentage of deep infections was on trees defoliated in May. At the time of the May defoliation there were few new shoots and the leaves were only about half-size. After defoliation, new shoots rapidly pushed out and the trees soon had such a leafy appearance that one might have expected this early defoliation to have less effect than the later ones, when many more leaves were removed and renewals were slow and sparse.

The harmful effect of early defoliation on the tree is in accord with the observation of the writer that severe late-spring pruning after foliation is well on the way has a stunting effect. The deleterious effect of early defoliation is further shown by the fact that in 1939 trees defoliated early in the previous 2 years were decidedly stunted in comparison with trees on all the other plots.

DISCUSSION

In the experiment in which inoculations were made at monthly periods for more than 1 year, the time of greatest infection was July. Infection rose rapidly to its maximum and declined very abruptly in August and September (fig. 1). The results of the present experiment indicate that temperature should not be considered the main contributing factor to the shape of the curve of infection. It is possible that some host condition was responsible for greater susceptibility in midsummer than at any other time. Other experiments (*1*) indicate that *Xylaria mali* infects much more readily when the host is in a low state of vigor, and this suggests that susceptibility may be associated with a seasonal diminution in the root activity of the host. Resistance or susceptibility to attack by a disease organism is not known to have been reported heretofore as a measure of seasonal root activity.

The relation of host condition to infection by the perennial apple canker pathogen (*Neofabraea perennens* (Zeller and Childs) Kienholz) was noted by Shear and Cooley (*8*). This fungus attacked twigs

during a very short period of the year, namely, in October, November, and December. This period of infectibility of apple twigs with this fungus corresponds in general to the period which Swarbrick (*10*) has shown to be the time of greatest starch accumulation and presumably of least activity of twigs as determined by carbohydrate changes. Results of the experiments reported in figure 1 indicate that there may be also a period of low vital activity of the roots and that maximum infectibility with a weak parasite such as *Xylaria mali* may indicate the time of the year when seasonal root activity of apple trees is lowest. Most of the reports of investigations on root development as determined by elongation show a period of greatly lessened activity during midsummer.

Kinman (*3*), working with drupaceous fruits in California, reported little or no root growth from June 1 to August 22. The physiological studies of Harris (*2*), Stevens (*9*), McDougall (*4*), and Rogers (*7*) on root activity of various tree species indicate that there is a period of relative inactivity in midsummer and a period of increased root activity in September and October. Reed and MacDougal (*6*) studied radial growth of orange trees in conjunction with shoot and root growth. Their data show a period of inactivity of the roots from early in June until about the middle of July. These periods of cessation of root activity of various plants correspond in general to the period of greatest susceptibility of apple roots to attack by *Xylaria mali*.

SUMMARY

Young apple trees in the nursery row were inoculated at monthly intervals from 1933 to 1935, inclusive, with the black root rot pathogen (*Xylaria mali*). In each year infection rose gradually to a maximum in July and declined greatly by September. It is suggested that the peak in infection may be related to a lessening of the metabolic activity of the roots in midsummer.

Maltreatment of the trees at monthly intervals, including cutting the trunk more than half through and bending the top over, ringing the trunk, root pruning, and summer pruning of branches, gave evidence that susceptibility to infection and the extent of the lesions are probably influenced by the seasonal activity of the trees. In general, the greatest effect of the maltreatments in increasing susceptibility was produced when the treatments were given in June and the inoculations made in July.

Artificial defoliation at periodic semimonthly periods was carried on for two summers and the residual effect was studied the third summer. Defoliation in general slightly increased susceptibility to the disease. Defoliations in the early part of the season resulted in more pronounced susceptibility to *Xylaria mali* and in a greater stunting of growth than defoliations in the latter part of the summer.

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EFFECTIVENESS OF SELECTION ON PROGENY PERFORMANCE AS A SUPPLEMENT TO EARLIER CULLING IN LIVESTOCK[1]

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INTRODUCTION

The extensive literature on the use of the progeny test in selecting breeding animals deals almost exclusively with its accuracy, as compared with that obtained from the use of pedigree, individual performance, or averages of collateral relatives, as an indicator of transmitting ability. Although several investigators, particularly Wright (*15*)[3] and Lush (*3, 4, 5*), have emphasized difficulties in the practical use of the progeny test, its accuracy under properly controlled conditions is unquestioned. However, from the standpoint of genetic progress expected from selection in a given period of time, the usefulness of the progeny test is greatly influenced by factors other than its relative accuracy. The most important of these are the age at which progeny tests can be obtained and the rate of reproduction. The longer interval between generations that results from use of the progeny test in selection tends to offset the advantage of more accurate selection and may actually reduce the rate of improvement obtained.

The purpose of this study is to examine the effectiveness of selection based on the progeny test when it is used to supplement earlier selection. The criterion of effectiveness is the average genetic improvement expected yearly from early selection alone as compared with that expected when use is made of the progeny test. The examples have been chosen to include economic traits in farm livestock for which the basis of earlier culling is restricted to individual performance, pedigree, or average performance of collateral relatives.

ANNUAL IMPROVEMENT EXPECTED FROM SELECTION IN CLOSED POPULATIONS

The two factors that determine annual improvement from selection in any closed population are (1) the average genetic superiority of those animals selected to become parents over the group from which they were chosen (ΔP) and (2) the average age of parents when their offspring are born or the average interval between generations (T). These averages are weighted according to the proportion of offspring from parents of different sex and age groups. Since ΔP represents the average genetic gain in T years, the average annual gain is $\Delta G = \frac{\Delta P}{T}$.

[1] Received for publication April 28, 1943.
[2] The authors are indebted to Prof. W. G. Cochran of Iowa State College for suggestions on statistical procedure.
[3] Italic numbers in parentheses refer to Literature Cited, p. 475.

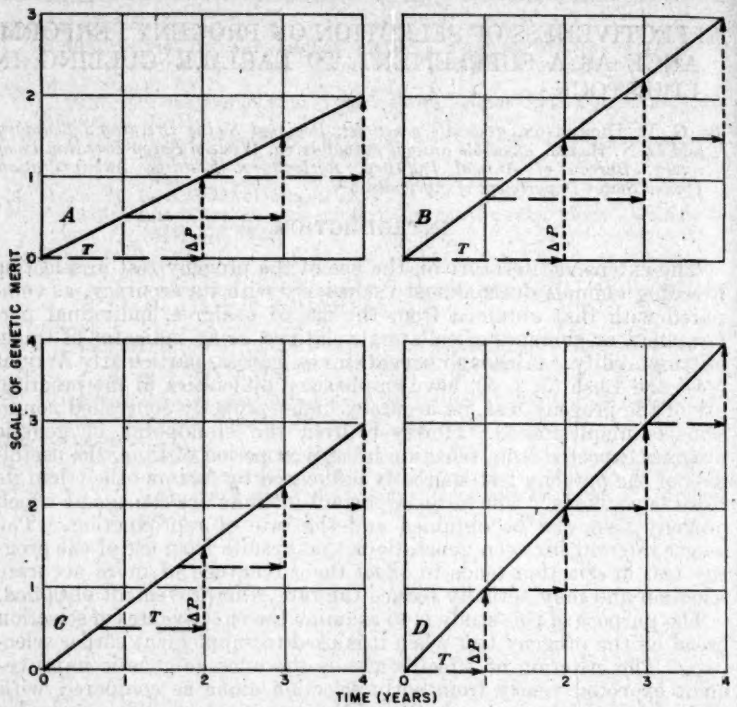

FIGURE 1.—Effect of interval between generations (T) and average genetic superiority of parents ($\triangle P$) on annual progress from selection ($\triangle G$). (Annual progress $=\Delta G=\frac{\Delta P}{T}$). *A*, $\frac{\Delta P}{T}=\frac{1}{2}=0.50$; *B*, $\frac{\Delta P}{T}=\frac{1.5}{2}=0.75$; *C*, $\frac{\Delta P}{T}=\frac{1}{1.33}=0.75$; *D*, $\frac{\Delta P}{T}=\frac{1}{1}=1.0$.

The most effective plan of making selections is the one that produces most improvement per unit of time. One plan may be more effective than another because it (1) increases ΔP and/or decreases T, (2) increases ΔP relatively more than T, or (3) decreases ΔP relatively less than T. The effect of changing ΔP and T is illustrated in figure 1.

The parents of the animals born in any one year differ in age and in the intensity of the selection applied to the different age groups and sexes. When the different parents within each age and sex group have equal opportunity to produce offspring, the average yearly genetic progress expected in two successive cullings of sires and of dams is [4]

$$\Delta G=\frac{\overbrace{N_1\Delta S_1+N_2(\Delta S_1+\Delta S_2)}^{\Delta P \text{ for sires}}+\overbrace{M_1\Delta D_1+M_2(\Delta D_1+\Delta D_2)}^{\Delta P \text{ for dams}}}{\underbrace{N_1Y_1+N_2Y_2}_{T \text{ for sires}}+\underbrace{M_1Z_1+M_2Z_2}_{T \text{ for dams}}} \qquad (1)$$

[4] This formula is rigorously proved algebraically from the fact that the average breeding value of an unselected group of offspring tends to be the same as that of the parents and may be extended to any number of successive cullings. The assumption is made that the average difference between offspring born in successive years (ΔG) is constant, as would be expected for polygenic traits in a closed population where a regular breeding plan was in use.

in which

ΔS_1=average genetic superiority of young sires retained in the first selection

N_1=proportion of the offspring that are from young sires

Y_1=average age of young sires when their offspring are born

ΔS_2=additional genetic superiority of sires obtained from the second culling of sires retained in the first selection

N_2=proportion of the offspring produced by sires retained in the second selection

Y_2=average age of sires saved in the second culling when their subsequent offspring are born

ΔD_1, M_1, Z_1, ΔD_2, M_2, and Z_2 have corresponding meanings for dams retained in the first and second cullings.

The general principles that govern progress from selection are the same for a whole breed as for a single closed herd. It is impractical to consider here the many forms that herd differences (genetic and environmental) may take, and they are ignored in the formulas for calculating ΔS_1, ΔS_2, etc. This procedure favors the progeny test, since the use of progeny averages helps to minimize errors in selection from random environmental variation within a herd but does not lessen those from environmental differences between herds unless a sire has progeny in more than one herd.

GENETIC SUPERIORITY FROM FIRST CULLING ($\triangle S_1$ and $\triangle D_1$)

In estimating the selection differential or average gain in apparent merit of a selected group as compared with the group from which it was chosen ($\bar{i}$), it is assumed that the basis of selection (I) is normally distributed and that all individuals below a given level are culled. The expected size of the differential or apparent gain in either sex depends on the proportion saved (p), as illustrated in figure 2. In

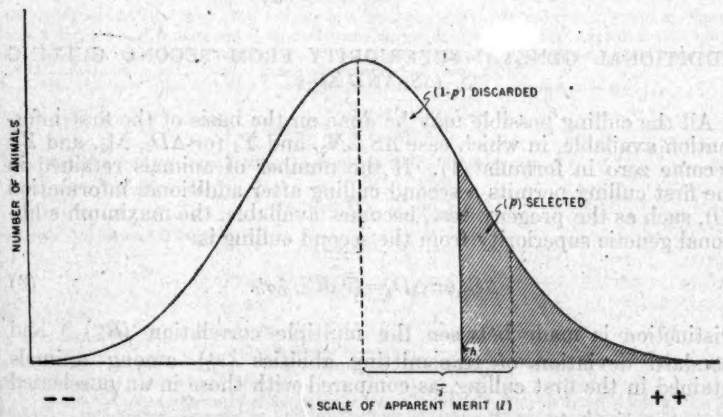

FIGURE 2.—A normal distribution showing how a population may be sharply divided at a point (h) into a selected (p) and a discarded (1-p) fraction. The average superiority in apparent merit of the selected fraction is ($\bar{i}$).

livestock breeding, p (and consequently $\bar{i}$) is largely determined by such factors as rate of reproduction, longevity, and age at puberty, peculiar to each type of livestock. Values of $\bar{i}$ in standard deviation units for different values of p are given for normally distributed populations of infinite size by Pearson (*10*) and may be calculated from Fisher and Yates (*1*) for smaller populations (from 2 to 50).

Since the selected group is chosen because of its superiority for some trait (X) or index (I_1) that is never perfectly correlated with transmitting ability (G), the average genetic superiority expected from the first selection is

$$\Delta S_1 \text{ or } \Delta D_1 = (\bar{i}_1) b_{GI_1} \sigma_{I_1} = (\bar{i}_1) r_{GI_1} \sigma_G. \qquad (2)$$

Here $\bar{i}_1$ represents the selection differential in standard deviation units, b_{GI_1} the regression of transmitting ability on apparent merit, r_{GI_1} the corresponding correlation, and σ_G the standard deviation of transmitting abilities. It is convenient to calculate r_{GI_1} and σ_G in terms of the hereditary and environmental portions of the observed variance of the population; for example, when the first selection is made on some phenotypic trait (X),

$$r_{GX} = \sqrt{\frac{G}{E+G}} = \sqrt{G}, \text{ and } \sigma_G = \sigma_X \sqrt{G},$$

where G is the heritability or fraction of the observed variance caused by individual differences in transmitting ability $\left(\frac{\sigma_G^2}{\sigma_X^2}\right)$ and E is the remaining fraction attributed to environment, dominance, and epistasis or gene interaction $\left(\frac{\sigma_E^2}{\sigma_X^2}\right)$.

ADDITIONAL GENETIC SUPERIORITY FROM SECOND CULLING (ΔS_2 AND ΔD_2)

All the culling possible may be done on the basis of the first information available, in which case ΔS_2, N_2, and Y_2 (or ΔD_2, M_2, and Z_2) become zero in formula (1). If the number of animals retained in the first culling permits a second culling after additional information (O), such as the progeny test, becomes available, the maximum additional genetic superiority from the second culling is

$$\Delta S_2 \text{ or } \Delta D_2 = (\bar{i}_2) R'_{G \cdot I_1 O} \sigma'_G. \qquad (3)$$

Distinction is made between the multiple correlation ($R'_{G \cdot I_1 O}$) and standard deviation of transmitting abilities (σ'_G) among animals retained in the first culling, as compared with those in an unselected

group ($R_{G.I_1O}$ and σ_G), because it is mathematically convenient to calculate the former in terms of the latter.[5]

The selection differential for the second culling ($\overline{i_2}$) can be calculated from table 20 of Fisher and Yates (*1*) since it is not affected materially by the slight skewness expected in the distribution of I_2.[6]

EFFECTIVENESS OF SELECTION FOR IMPORTANT TRAITS OF FARM ANIMALS

A regular plan of progeny testing may be effective in increasing rate of progress in one kind of animal but not in another even for similar traits, or for one kind of trait but not for another in the same population. The effectiveness depends largely on the age of parents when progeny-test information becomes available, but to some extent also on the rate of reproduction and the relative accuracy of information used for the first culling. Obviously these factors differ for particular kinds of animals and traits.

Several examples that illustrate the influence of these factors on the effectiveness of the progeny test have been chosen. These examples were selected because of their economic importance and because of the extensive breeding research that is being directed toward their improvement. They illustrate the effectiveness of the progeny test when used in conjunction with earlier selection based on pedigree, on individual performances, and on performance of collateral relatives, each of these plans being peculiarly fitted to making early selections for a different kind of trait.

TRAITS MEASURED IN BOTH SEXES BEFORE BREEDING AGE

Many important traits, such as growth rate, economy of feed utilization, market conformation, fleece weight, and fleece length, can be

[5] The standard deviation of transmitting abilities among the group saved in the first culling is

$$\sigma'_G=\sigma_G\sqrt{1-r^2_{GI}\,(1-\sigma_s^2)}$$

where σ_s^2 is the fraction of the original variance of I_1 that remains in the selected group. Values of σ_s^2 (hereafter designated as σ_{ss}^2 for sires and σ_{sd}^2 for dams) may be calculated for large populations from the formula $\sigma_s^2=1-\bar{i}_1(\bar{i}_1-h)$, suggested by Professor Cochran, where h is the plus or minus deviation from the mean of the unselected population at the point of truncation of the normal curve (fig. 2).

The multiple correlation of G with O and I_1 among animals retained in the first culling is

$$R'_{G.OI_1}=\sqrt{\frac{r'^2_{GI_1}+r'^2_{GO}-2r'_{GI_1}r'_{GO}}{1-r'^2_{GI_1}r'^2_{GO}}}$$

The correlation between G and I_1 among those selected in the first culling is

$$r'_{GI_1}=r_{GI_1}\sqrt{\frac{\sigma_s^2}{1-r^2_{GI_1}(1-\sigma_s^2)}}$$

whereas that between G and O is

$$r'_{G_sO_s}=r_{G_sO_s}\sqrt{\frac{1-r^2_{GI_1}(1-\sigma^2_{ss})}{1-r^2_{GI_1}r^2_{G_sO_s}(1-\sigma^2_{ss})-r^2_{GI_1}r^2_{G_dO_s}(1-\sigma^2_{sd})}}$$

for sires, and

$$r'_{G_dO_d}=r_{G_dO_d}\sqrt{\frac{1-r^2_{GI_1}(1-\sigma^2_{sd})}{1-r^2_{GI_1}r^2_{G_sO_d}(1-\sigma^2_{ss})-r^2_{GI_1}r^2_{G_dO_d}(1-\sigma^2_{sd})}}$$

for dams.

[6] The exact selection differential expected in the second culling ($\overline{i_{12}}$) of a population of infinite size was calculated by a method, suggested by Professor Cochran, for varying proportions retained in the first (p_1) and second (p_2) culling and for different degrees of correlation between I_1 and I_2 in the unselected population. Even when $r_{I_1I_2}$ is as large as 0.8, the exact value of $\overline{i_{12}}$ expected does not differ appreciably, because of skewness, from that expected for a normal distribution unless p_2 is much larger or smaller than 0.5. For example, when $p_1=0.2$, $p_2=0.1$, and $r_{I_1I_2}=0.8$, the exact expectancy for $\overline{i_{12}}$ is only 3 percent higher than for a normal distribution. In the examples that follow, p_2 is never larger than 0.5 nor smaller than 0.1 and $r_{I_1I_2}$ does not exceed about 0.8.

measured on both males and females before they reach breeding age. The annual progress expected from selection based on individual performance alone in swine and sheep as compared with that expected from the supplementary use of the progeny test is indicated in the examples that follow.

When first selections are based on individual performance (X) alone, the genetic superiority expected from the first selection is

$$\Delta S_1 \text{ or } \Delta D_1 = (\bar{i}_1) G \sigma_X. \tag{4}$$

When second selections are based on the optimum combination of individual performance and progeny test (formula 3), the additional genetic superiority expected is

$$\Delta S_2 = (\bar{i}_2) G \sigma_X \sqrt{\sigma^2_{ss} + \frac{nd(1-G)^2}{4(A+nB)+ndG(1-G)-nG^2(1-\sigma^2_{sd})}} \tag{5}$$

for sires, and

$$\Delta D_2 = (\bar{i}_2) G \sigma_X \sqrt{\sigma^2_{sd} + \frac{n(1-G)^2}{4(A+nB)+nG(1-G)-nG^2(1-\sigma^2_{ss})}} \tag{6}$$

for dams, each of which produces one litter of n progeny. The symbols and their interpretations in terms of the hereditary and environmental fractions of the variance are as follows:

L=fraction of total variance due to differences in environment and in gene interaction that are alike for members of the same litter

E=fraction that behaves as random environmental variation between litter mates

A=fraction due to differences between litter mates=$E+G/2$

B=fraction due to differences between paternal half-sibs, less A=$L+G/4$

C=fraction due to differences between nonsibs, less $A+B$=$G/4$, so that $G+L+E=A+B+C=1$

In addition,

n=number of offspring per litter, and

d=number of litters per sire.

Weight at 180 days may be used as an example for swine, in which $G=0.30$, $L=0.20$, $E=0.50$, and $\sigma_x=32$ pounds, in accord with values found by Whatley (*14*) and Hazel (*2*). We shall consider a 20-sow herd in which breeding stock are saved from the spring farrow only and $n=5$. The age when offspring are born is 1 year for young boars and gilts and 2 years for the tested boars and sows. The selection differentials for formulas (4), (5), and (6) are calculated from table 20 of Fisher and Yates (*1*). For example, if 3 young sires are saved annually, $p=3/50$, so that, for sires, $(\bar{i}_1)=1.91$. When the best 1 of the 3 is kept after testing, $p=1/3$ and $(\bar{i}_2)=0.85$. The curves for annual progress in figure 3 were constructed from formula 1. Solid lines show progress expected from the use of 2, 3, and 4 young sires and 1 boar tested the year before, when no tested sows are used ($M_2=0$), but the proportion of the litters by the tested boar (N_2) varies from 0 to 0.8. Broken lines show progress expected as the

proportion of litters farrowed by 2-year-old sows (M_2) varies from 0 to 0.5, when all litters are sired by 2 young boars ($N_2=0$).

Figure 3, *A*, (solid lines) shows that ΔG is maximum when 2 young sires are used each year on all sows. The use of 3 or 4 young sires decreases progress, as does increasing the proportion of offspring by tested sires. The use of 1 young sire instead of 2 would not increase ΔG since all offspring would then be paternal half-sibs, and the reduced genetic variability and heritability would more than cancel the slightly larger selection differential. Even a plan of testing the optimum number of 6 to 8 sires in an auxiliary herd of 20 sows and using the 2 best ones in the closed herd does not increase ΔG, as shown at the extreme right of figure 3, *A*. This indicates that the progeny test for sires is not effective for this or similar traits in swine, regardless of herd size.

Figure 3, *A*, (broken lines), also shows that ΔG is about the same when the optimum proportion of the litters (10 to 20 percent) is from

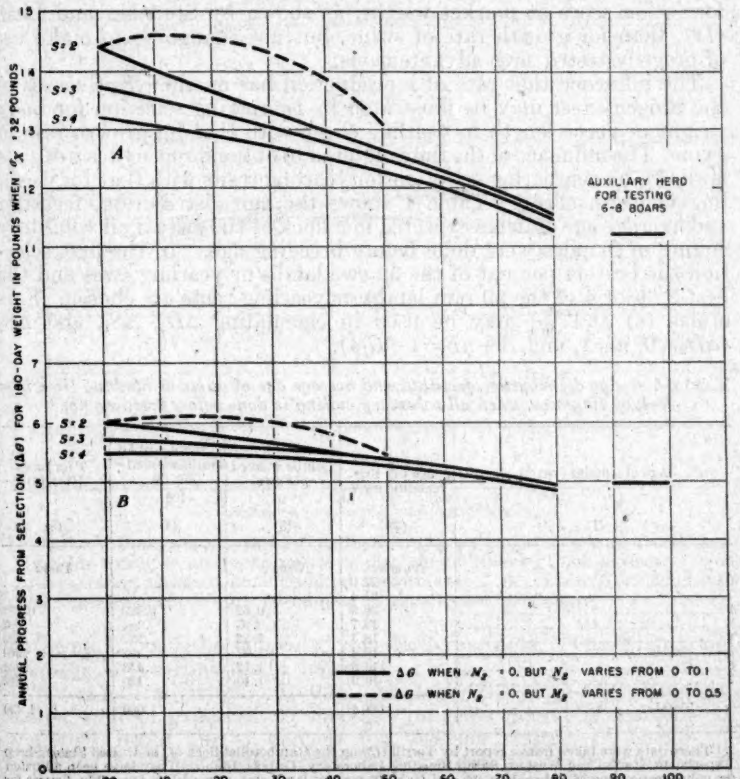
S=2
S=3
S=4
A
AUXILIARY HERD FOR TESTING 6-8 BOARS
S=2
S=3
S=4
B
ANNUAL PROGRESS FROM SELECTION (ΔG) FOR 180-DAY WEIGHT IN POUNDS WHEN σx = 32 POUNDS
ΔG WHEN N2 = 0, BUT N2 VARIES FROM 0 TO 1
ΔG WHEN N2 = 0, BUT M2 VARIES FROM 0 TO 0.5
PROPORTION OF OFFSPRING FROM TESTED SIRES OR DAMS (N2 OR M2)

FIGURE 3.—Effect of progeny testing on genetic progress from selection for 180-day weight in a closed 20-sow herd of swine, when early culling is based on individual weights. *A*, When $G=0.30$, $L=0.20$; *B*, when $G=0.125$, $L=0.25$. s=number of sires tested each year.

tested sows as when only gilts are used. As M_2 is increased, the first selection of gilts becomes more effective, the second selection of sows becomes less effective, and the average age of dams increases. Up to $M_2=0.2$ the opposing influences nearly cancel, but as M_2 is increased further, progress declines.

It is apparent from formulas (5) and (6) that progeny testing is more likely to increase progress for traits of lower heritability (G smaller, E larger) that are unaffected by litter environment ($L=0$, $B=G/4$). As a population becomes more unform genetically owing to inbreeding (f), heritability declines (that is, $G \cong \frac{G_o(1-f)}{1-G_o f}$). For example, as f rises from 0 to 0.67, the heritability (G) of growth rate in swine would change roughly from 0.30 to 0.125, L from 0.20 to 0.25, and E from 0.50 to 0.625. Figure 3, B, shows that progeny testing of boars or sows does not increase ΔG even at this lower level of heritability, although the reduction in ΔG from the use of a tested boar is less marked. G and L appear to be a little smaller for conformation score at market weight, as shown by Stonaker and Lush (*12*), than for growth rate of swine, but not enough so to make use of progeny-tested sires advantageous.

The influence that rate of reproduction has on the effectiveness of the progeny test may be illustrated by comparing selection for body weight or fleece length in yearling sheep with that for growth rate in swine. The influence of the time required to obtain progeny tests of sires is shown by comparing selection for yearling traits with that for weanling traits in sheep. Table 1 shows the age distribution, fertility, and average age of dams expected in a flock of 100 ewes if all voluntary culling of females were done before breeding age. In the first selection the best 44 percent of the 50 ewe lambs or yearling ewes and the best 2, 3, or 4 of the 50 ram lambs or yearling rams are chosen. Formulas (4) and (5) may be used in calculating ΔD_1, ΔS_1, and ΔS_2 ($\Delta D_2=0$, $n=1$, and $A+nB=1-G/4$).

TABLE 1.—*Age distribution, fertility, and average age of dams at lambing time in a flock of 100 ewes, when all voluntary culling is done before breeding age* [1]

Age of females (years) (1)	Ewes of each age per 100 breeding ewes (2)	Lambs weaned per ewe (3)	Fraction of all lambs weaned = $\frac{(2)\times(3)}{100}$ (4)	T for ewes [(1)×(4)] (5)
	Number	*Number*		*Years*
0	22.0			
1	21.4			
2	20.9	0.62	0.129	0.259
3	19.7	.93	.184	.552
4	18.3	1.22	.222	.893
5	16.4	1.17	.192	.960
6	13.8	1.12	.153	.924
7	10.9	1.10	.120	.842
Total	143.4		1.000	4.430

[1] These data were taken from a report by Terrill (*13*) on the Rambouillet flock of the United States Sheep Experiment Station and Western Sheep Breeding Laboratory, Dubois, Idaho. They have been adjusted for voluntary culling after breeding age and for a 100-percent lamb crop at weanling age. The figures for ewe lambs and yearling ewes represent those necessary for replacements.

Figure 4, A, shows yearly progress for weanling (solid lines) and for yearling (broken lines) traits when heritability is 0.30 and rams are used first as yearlings. Use of the best ram tested the year before

on the optimum proportion (0.6 to 0.7) of the ewes increases progress by about 4 percent for weanling traits but reduces progress for yearling traits, as compared with the use of only the 2 best yearling rams each year. The difference occurs solely because selection of rams on progeny performance can be made a year earlier for weanling than for yearling traits. As shown at the extreme right of the figure a still greater increase in progress (6 percent) could be obtained for weanling traits by testing the optimum number (7) of yearling rams each year in an auxiliary flock of 100 ewes and using the 2 best ones

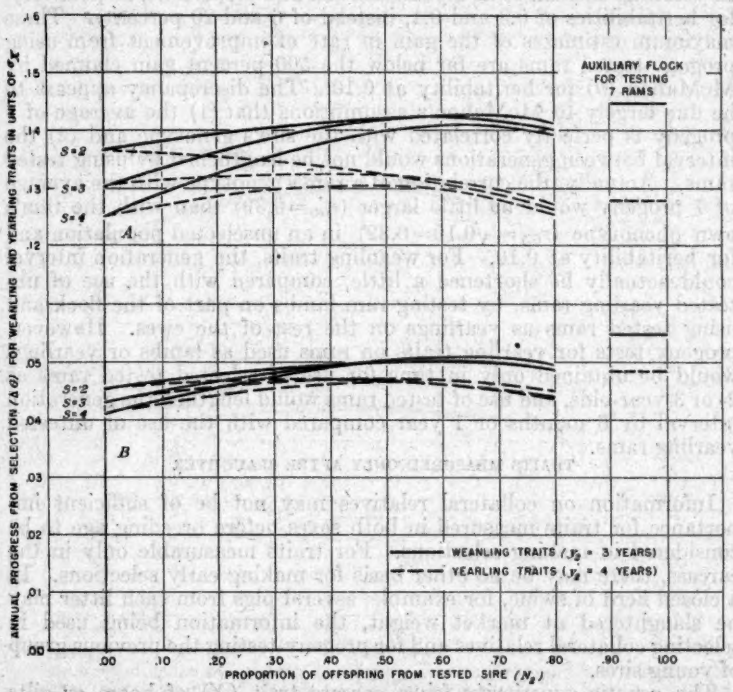

FIGURE 4.—Influence of progeny testing of rams on genetic progress from selection for weanling and yearling traits in a closed 100-ewe flock of sheep, when early culling is based on individual performance. *A*, When $G=0.30$, $L=0$; *B*, when $G=0.10$, $L=0$. s=number of sires tested each year.

in the main flock the following year as 2-year-olds. This plan is not effective for yearling traits, however.

When heritability is only 0.10 (fig. 4, *B*) use of the best progeny-tested ram is expected to increase progress about 11 percent for weanling traits and 3 percent for yearling traits. By using the auxiliary flock for testing rams, the increase in progress would be raised to 20 percent for weanling traits and 5 percent for yearling traits.

Progress for weanling traits could be increased still further by testing each of the best ram lambs on a small number of ewes and then using the best tested rams as yearlings instead of as 2-year-olds.

For example, suppose the 4 best ram lambs were tested on 40 ewes and the remaining 60 ewes were mated to the best yearling ram tested the year before. Under this plan, yearly progress expected would be 20 and 28 percent greater, for heritabilities of 0.3 and 0.1, respectively, than if the 2 best untested yearling rams were used on the entire flock, whereas the advantage of testing yearling rams and using the best tested 2-year-old is only 4 and 11 percent, respectively. The increase in progress from testing rams in the auxiliary flock of 100 ewes is also greater if the tested rams can be used in the main flock as yearlings instead of as 2-year-olds (22 and 37 percent, respectively, for heritabilities of 0.3 and 0.1, instead of 6 and 20 percent). These maximum estimates of the gain in rate of improvement from using progeny-tested rams are far below the 500 percent gain claimed by McMahon (*9*) for heritability at 0.10. The discrepancy appears to be due largely to McMahon's assumptions that (1) the average of 7 progeny is perfectly correlated with the sire's genotype and (2) the interval between generations would not be lengthened by using tested rams. Actually, the correlation of a ram's genotype with the average of 7 progeny would be little larger ($r_{GO}=0.39$) than with the ram's own phenotype ($r_{GX}=\sqrt{0.10}=0.32$), in an unselected population and for heritability at 0.10. For weanling traits, the generation interval could actually be shortened a little, compared with the use of untested yearling rams, by testing ram lambs on part of the flock and using tested rams as yearlings on the rest of the ewes. However, progeny tests for yearling traits on rams used as lambs or yearlings would be obtained only in time for use of selected tested rams as 2- or 3-year-olds, and use of tested rams would lengthen the generation interval by 6 months or 1 year compared with the use of untested yearling rams.

TRAITS MEASURED ONLY AFTER SLAUGHTER

Information on collateral relatives may not be of sufficient importance for traits measured in both sexes before breeding age to be considered in making selections. For traits measurable only in the carcass, there may be no other basis for making early selections. In a closed herd of swine, for example, several pigs from each litter may be slaughtered at market weight, the information being used in selecting collateral relatives and for progeny-testing the previous group of young sires.

The genetic superiority for a carcass trait (X) of boars or gilts selected in the first culling based on the average of n litter mates is

$$\Delta S_1 \text{ or } \Delta D_1=\bar{(i_1)}\frac{G}{2}\sigma_X\sqrt{\frac{n}{A+n(B+C)}}. \qquad (7)$$

The additional genetic superiority from the second culling based on the optimum combination of the average of nd progeny and of n litter mates is

$$\Delta S_2=\bar{(i_2)}\frac{G}{2}\sigma_X\cdot$$

$$\sqrt{\frac{n}{A+n(B+C)}\left[\sigma_u^2+\frac{d(A+nB)^2}{(A+nB+ndC)[A+n(B+C)]-n^2C^2(d+1-\sigma_u^2)}\right]} \qquad (8)$$

for sires, and

$$\Delta D_2 = \overline{(i_2)} \frac{G}{2} \sigma_x \sqrt{\frac{n}{A+n(B+C)} \left\{ \sigma_{sd}^2 + \frac{(A+nB)^2}{[A+n(B+C)]^2 - nC^2(2-\sigma_{ss}^2)} \right\}} \quad (9)$$

for dams having only one litter. The symbols used are those defined for formulas (4) to (6).

The curves in figure 5 are for a closed 20-sow herd in which carcass traits are observed on 2 pigs from each litter and when the s young boars and the gilts used for breeding each year are chosen from 40

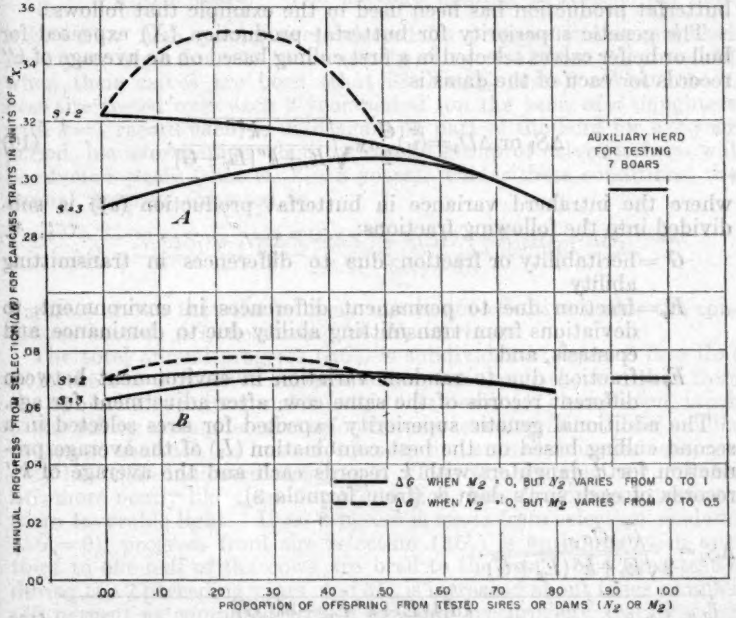
ANNUAL PROGRESS FROM SELECTION (ΔD) FOR CARCASS TRAITS IN UNITS OF σ_x
.36
.34
.32
.30
.28
.08
.06
.04
.02
.00
S=2
S=3
A
B
AUXILIARY HERD FOR TESTING 7 BOARS
ΔG WHEN N_2 = 0, BUT N_2 VARIES FROM 0 TO 1
ΔG WHEN N_2 = 0, BUT N_2 VARIES FROM 0 TO 0.5
.00 .10 .20 .30 .40 .50 .60 .70 .80 .90 1.00
PROPORTION OF OFFSPRING FROM TESTED SIRES OR DAMS (N_2 OR M_2)

FIGURE 5.—Influence of progeny testing on genetic progress from selection for carcass traits in a closed 20-sow herd of swine, when the first culling is based on averages for 2 litter mates. *A*, When $G=0.50$, $L=0$; *B*, when $G=0.10$, $L=0$. s=number of sires tested per year.

gilts in 20 litters and 10 boars in 10 litters. Use of the best sire tested the preceding year reduces progress expected when heritability is 0.50 (fig. 5, *A*), although progress is increased about 10 percent if optimum proportion of the litters (about 0.2) is from the best sows tested the year before. When heritability is as low as 0.10 (fig. 5, *B*), the progeny test is slightly effective. As shown at the extreme right of figure 5, progress is not increased by testing the optimum number (7) of boars in an auxiliary herd of 20 sows and using the best 2 in the main herd the next year.

Thus it seems unlikely that progeny testing can increase progress for carcass traits in swine appreciably if earlier culling of breeding animals can be based on the average performance of several litter

mates. However, progeny tests are much more likely to be helpful in selecting for such traits in beef cattle or sheep, where the reproductive rate is lower and earlier culling must be based on the performance of half-sibs rather than full sibs.

REPEATABLE TRAITS EXPRESSED ONLY IN THE FEMALE

Progeny testing of sires might be presumed to have special usefulness in selecting for such traits as butterfat production in dairy cattle or prolificacy in swine, since early culling must be based largely on pedigree. Because progeny tests have received so much attention both in the literature and in the practice of dairy-cattle improvement, butterfat production has been used in the example that follows.

The genetic superiority for butterfat production (X) expected for bull or heifer calves selected in a first culling based on an average of k'' records for each of the dams is

$$\Delta S_1 \text{ or } \Delta D_1 = (\bar{i}_1)\frac{G}{2}\sigma_x\sqrt{\frac{k''}{E_r+k''[E_p+G]}}, \qquad (10)$$

where the intraherd variance in butterfat production (σ_x^2) is subdivided into the following fractions:

G = heritability or fraction due to differences in transmitting ability

E_p = fraction due to permanent differences in environment, to deviations from transmitting ability due to dominance and epistasis, and

E_r = fraction due to random variation in environment between different records of the same cow, after adjustment for age.

The additional genetic superiority expected for sires selected in a second culling based on the best combination (I_2) of the average production for d daughters with k records each and the average of k'' records of each sire's dam is (from formula 3)

$$\Delta S_2 = \frac{(\bar{i}_2)G\sigma_x}{2\sqrt{E_r+k''(E_p+G)}}\cdot$$

$$\sqrt{k''\sigma_{ss}^2+\frac{kd[4(E_r+k''E_p)+3k''G]^2}{4[E_r+k''(E_p+G)][4(E_r+kE_p)+kG(d+3)]-kk''G^2(d+1-\sigma_{sd}^2)}}. \qquad (11)$$

The additional genetic superiority expected for dams selected in a second culling based on the best combination of each cow's own average for k' records and her dam's average for k'' records is

$$\Delta D_2 = \frac{(\bar{i}_2)G\sigma_x}{2\sqrt{E_r+k''(E_p+G)}}\cdot$$

$$\sqrt{k''\sigma_{sd}^2+\frac{k'[4(E_r+k''E_p)+3k''G]^2}{4[E_r+k''(E_p+G)][E_r+k'(E_p+G)]-k'k''G^2}}. \qquad (12)$$

The results to be expected from progeny testing of dairy sires are shown in figure 6 for a closed herd of 120 cows. Heritability (G) is 0.25 in figure 6, A, and 0.10 in B, but repeatability ($G+E_p$) is 0.35 in both. These are roughly the upper and lower limits of herita-

bility indicated in such studies as those of Lush, Norton, and Arnold (*7*) and Lush and Straus (*8*). In this example, one-fourth of the cows are replaced each year; only calves from three-fourths of the cows that have completed one or more records are considered in selecting breeding animals; and 90 percent of the cows raise calves each year. Three-fourths of the heifer calves (30/40) are saved in the first culling and kept for two lactations, after which one-half (15/30) are retained in the second culling for an average of 4 more lactations. Thus the average age of dams when the calves from which breeding stock are chosen (second record and later) are born is about 4⅞ years; that is, $\frac{3 \text{ years}}{3}+\frac{7}{8}$ (5.5 years). The average number of records per dam is $k''=2\frac{7}{8}$. Also, young sires selected for progeny testing and used for 1 year when from 15 to 27 months of age are about 2½ years old when their calves are born (that is, $Y=2\frac{1}{2}$ years). When the 1 best sire tested over each 2-year period (on the basis of d daughters with $k=1$ record each) is used again on part of the herd for a 2-year period, his average age when his second group of calves is born will be about 8 years (that is, $Y_2=8$ years). Under these conditions, the annual progress expected is

$$\Delta G_t=\frac{N_1(\Delta S_1)+N_2(\Delta S_1+\Delta S_2)+\frac{1}{8}(\Delta D_1)+\frac{7}{8}(\Delta D_1+\Delta D_2)}{2.5N_1+8N_2+4\frac{7}{8}}.$$

Figure 6 shows that the progeny test is not effective under the conditions stated, ΔG_t decreasing as N_2 increases.

The total annual progress (ΔG_t) is subdivided in figure 6 into that from the two successive cullings among females (ΔG_d) and that from the two cullings among males (ΔG_s). As Seath (*11*) has shown, much of the culling among females is for disease, breeding failure, and similar causes, so that ΔG_d for butterfat production actually may be considerably less than indicated in figure 6. This would make the curves for ΔG_t more nearly like those for ΔG_s, which show the progeny test in a more favorable light. If no progress is made from selection of dams ($\Delta G_d=0$), progress from sire selection (ΔG_s) is optimum when one-third to one-half of the cows are bred to the best 1 of 4 sires tested during the 2 preceding years, and ΔG_t is increased about twice as much (10 percent as compared with 5 percent) by progeny testing when heritability is 0.10 as when heritability is 0.25.

Use of progeny-tested dairy sires would be a little more likely to increase the rate of improvement if, instead of the average production of the daughters alone being used, that of the dams to which each sire was mated were also considered properly. This procedure, according to Lush (*6*), would make progeny tests in a population of many herds about 1.12 to 1.20 times as accurate as the use of the average production of the daughters alone. The exact amount depends largely on the correlation between the average production of the sire's daughters and that of their dams, and would, therefore, be less for comparisons between sires tested in the same herd and during the same years. In the above example (when selection of dams is presumed ineffective), increasing the accuracy of progeny tests 1.10 times would change the percentage increase in yearly improvement resulting from optimum use of tested sires only, from 10 to 13 if heritability is 0.10 and from 5 to 8 if heritability is 0.25.

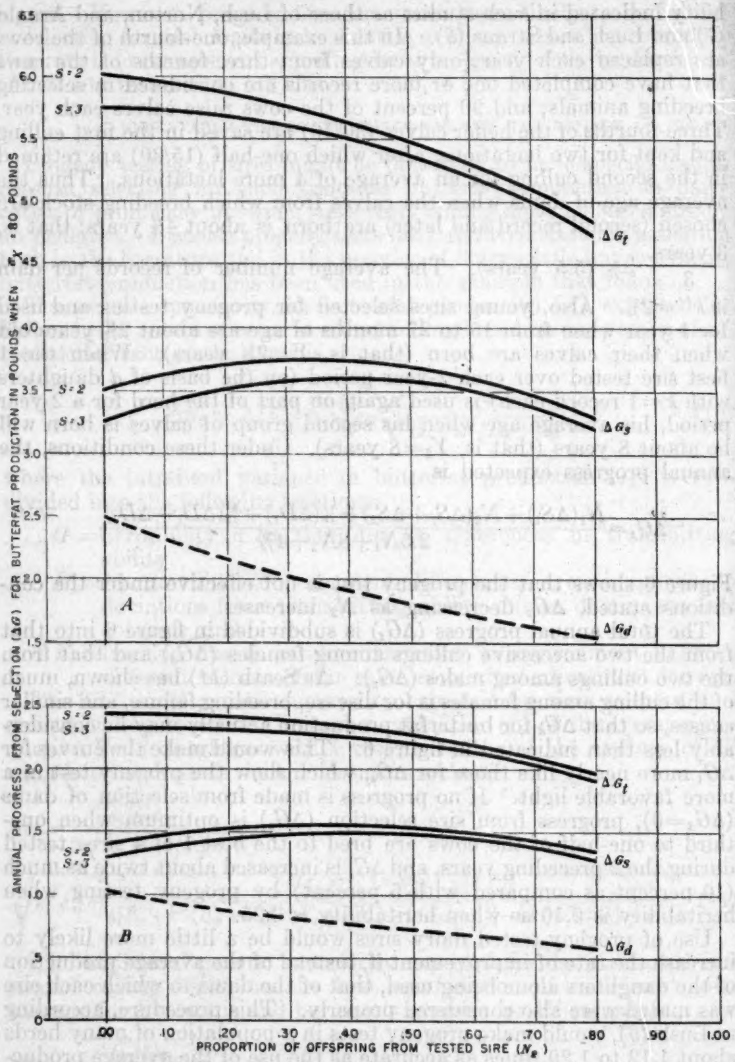

FIGURE 6.—Effect of using progeny-tested sires on genetic progress from selection for butterfat production in a closed 120-cow herd, when early culling i based on the dam's average production alone. *A*, When $G=0.25$, $E_p=0.10$; *B*, when $G=0.10$, $E_p=0.25$. s=number of sires tested each year.

DISCUSSION

The foregoing examples indicate that the possibilities of increasing progress by a regular plan for use of progeny-tested sires are limited to certain kinds of livestock and to certain traits. The reasons for this limitation may be illustrated by comparing the effectiveness of

progeny testing in the different examples. First, the less the interval between generations is increased by progeny testing the more likely it is that progeny testing will increase progress. This is shown by contrasting the results of selecting for weanling and yearling traits in sheep (fig. 4). The only difference in these examples is that 1 year is required to obtain progeny-test information on weanling traits, whereas 2 years are required for yearling traits. Second, when the rate of reproduction is low, progeny testing of sires is more likely to increase progress. The resulting increase in genetic superiority of parents (ΔP) tends to be larger, relative to that in the age of parents (T), when there is less opportunity for early culling, particularly among females. This is the reason that progeny testing affects progress more favorably for yearling traits in sheep (fig. 4) than for growth rate in swine (fig. 3), and when little voluntary culling of females is possible for butterfat production in dairy cattle (ΔG, in fig. 6). Third, if the basis for making first selections is relatively inaccurate, the progeny test is more likely to be effective, because there is more environmental variation to be discounted by the progeny test and more of the genetic variation remains among animals tested. This is illustrated by the contrast in the effectiveness of the progeny test for high and low heritability (figs. 3, 4, 5, and 6).

Thus a combination of circumstances, largely beyond the breeder's control, operates to make the use of a regular plan of progeny testing a wise or unwise procedure. In many cases when the progeny test is most easily applied it may actually reduce genetic progress (fig. 3). Even when the circumstances indicate the use of progeny-tested sires, there is danger that its full effectiveness will not be realized in practice because of unwise judgment. Too many or too few young sires may be tested on too many or too few females, so that the optimum use of young and tested sires is not attained (fig. 4). Although little attention has been given to this point, it becomes important once a breeder decides to use a regular plan of progeny testing.

The progeny test is not likely to be more effective in increasing genetic progress in actual practice than under the conditions assumed in the foregoing examples. Where assumptions had to be made, these generally favored the progeny test. For example, the average of a sire's offspring was assumed to be unbiased because of special treatment or selection among the offspring before the trait (X) was measured. Although the sharp truncation assumed here is not likely to exist in actual practice, particularly for any single trait, this seemingly overestimates the selection differential for all age groups in both sexes. This favors the older animals, since more culling for age, sterility, disease, and other factors and more deaths would occur among them.

It was necessary to assume that the genetic gain from the first and the second selections (ΔS_1 and ΔS_2 or ΔD_1 and ΔD_2) was constant from year to year. Of course, this would not be exactly true, particularly for small herds. Nevertheless, the estimates of ΔG in the foregoing examples represent the average expectancy for any of the plans for regular use of progeny-tested sires. The effectiveness of progeny testing would be somewhat greater than indicated in these examples if a tested sire were used only when one of exceptional merit was found, or if the proportion of the herd mated to the tested sire were varied according to his apparent superiority. Although there are

some notable cases in which the progeny test has identified animals of exceptional transmitting ability, these cases are rare in breed histories and offer uncertain possibilities to the individual breeder who can test only a limited number of sires. Breeders who regularly use the best young sires extensively would be better able to recognize and make use of the occasional outstanding sire, if still available, than breeders who regularly use a tested sire on most of the herd and use young sires sparingly.

For simplicity, selection for one trait at a time was considered in the examples. Methods have been developed by Hazel (*2*) for expressing net merit as a linear function of several traits, including the performance of relatives. The relative effectiveness of the progeny test in selecting for an index based on several traits would be much the same as that for a single trait. In fact, the formulas developed herein for individual traits could be applied directly to more complicated cases by considering the index as a single trait.

The effect of progeny testing on the genetic progress in an entire breed is much the same as in a closed herd. A breed is just a much larger closed herd, in which another source of variation, herd differences, must be considered and in which inbreeding may be a negligible factor. Thus the same general conclusions for selection within closed herds apply for the much larger closed population of an entire breed. The regular use of progeny tests does not increase, and may decrease, the rate of progress unless the progeny-test information can be obtained early, the reproductive rate is low, and there is little or no basis for earlier culling.

These conclusions do not conflict in any way with the fact that unbiased progeny-test information always increases the accuracy of selection for traits that are influenced much by dominance, epistasis, or environmental variations. They simply mean that in the time required to carry out the progeny test the genetic progress from selection based on pedigree, individual merit, or family averages may be more than that obtained from selection on the progeny test. For the improvement of most traits, in most kinds of livestock, these conclusions point unmistakably toward the fuller use of pedigree, individual merit, and family averages for early culling in order to keep the interval between generations short and progress maximum.

The technique of artificial insemination may increase the advantage of using selected progeny-tested sires if the population is sufficiently large and if the reproductive rate of males is increased markedly thereby, as in sheep and cattle. If fewer sires are needed, more progress is expected from the more intense selection of young sires. However, mating each young sire to larger numbers of females also is likely to increase the accuracy of selecting between tested sires more than enough to offset the increased intensity selection of young sires, particularly for traits low in heritability.

In the literature, progeny testing does not always refer to use of progeny-tested individuals. The progeny-test breeding so successfully practiced on laboratory animals, poultry, and plants is often based on selection between and within the progenies themselves rather than between parents on the basis of the progeny test, and consequently does not increase the interval between generations. Actually, this is selection based on a combination of individual performance and family average. It differs from the methods indicated for farm live-

stock only in the greater emphasis on selection between families or progenies which a higher reproductive rate permits.

SUMMARY AND CONCLUSIONS

Annual improvement from selection in a closed herd or breed is the ratio of the average genetic superiority of parents (compared with the unselected group from which they were chosen) to the average age of parents when offspring are born.

Examples of progress expected from selection based on pedigree, individual performance, or averages for collateral relatives, with and without the supplementary use of the progeny test, have been given for representative economic traits of farm animals.

A regular plan of progeny testing is unlikely to increase, and may reduce, progress unless (1) the progeny-test information becomes available early in the tested animal's lifetime, (2) the reproductive rate is low, and (3) the basis for making early selections is relatively inaccurate. These factors are largely beyond the breeder's control, being relatively unchangeable for a particular kind of animal and trait.

Opportunity for improvement from selection is nearly maximum for most traits when (1) culling is based on individual performance, family average, and pedigree and (2) the interval between generations is kept short. Possible exceptions are weanling traits in sheep and carcass traits in sheep and beef cattle.

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